



Research

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Mates but not sexes differ in migratory niche in a monogamous penguin species

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Strong pair bonds generally increase fitness in monogamous organisms, but may also underlie the risk of hampering it when re-pairing fails after the winter season. We investigated whether partners would either maintain contact or offset this risk by exploiting sex-specific favourable niches during winter in a migratory monogamous seabird, the southern rockhopper penguin *Eudyptes chrysocome*. Using light-based geolocation, we show that although the spatial distribution of both sexes largely overlapped, pair-wise mates were located on average 595 ± 260 km (and up to 2500 km) apart during winter. Stable isotope data also indicated a marked overlap between sex-specific isotopic niches ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) but a segregation of the feeding habitats ($\delta^{13}\text{C}$ values) within pairs. Importantly, the tracked females remained longer (12 days) at sea than males, but all re-mated with their previous partners after winter. Our study provides multiple evidence that migratory species may well demonstrate pair-wise segregation even in the absence of sex-specific winter niches (spatial and isotopic). We suggest that dispersive migration patterns with sex-biased timings may be a sufficient proximal cause for generating such a situation in migratory animals.

1. Introduction

In 1758, the Swedish taxonomist Carl Linnaeus named the passerine bird chaffinch *Fringilla coelebs* (meaning 'bachelor finch') because he would mainly observe males throughout winter, whereas females migrated to lower latitudes (in [1]). For monogamous species, such sex-based segregation increases the risk of failure to re-unite partners in the subsequent breeding season, and may therefore considerably reduce fitness [2]. It is generally assumed that this potentially risky strategy would be offset by the exploitation of sex-specific, specialized niches, in which each partner may increase foraging gains and/or adjust timing of return compared with a shared-niche situation [3].

In seabirds, which can mate for life [4], it is generally unknown whether partners maintain close contact while at sea until the next breeding season. Recent surveys showed that partners may migrate to similar wintering areas, but without providing evidence for either close contact or segregation once there [5]. Here, we focused on the southern rockhopper penguin *Eudyptes chrysocome*. Eudyptid penguins are serially monogamous [6], despite undertaking long-range migrations during winter [7,8]. Recent progress made in miniaturized archival light-level geolocators has enabled the tracking of penguins at sea over the complete non-breeding season, with minimal disturbance [7,8]. We combined this spatial

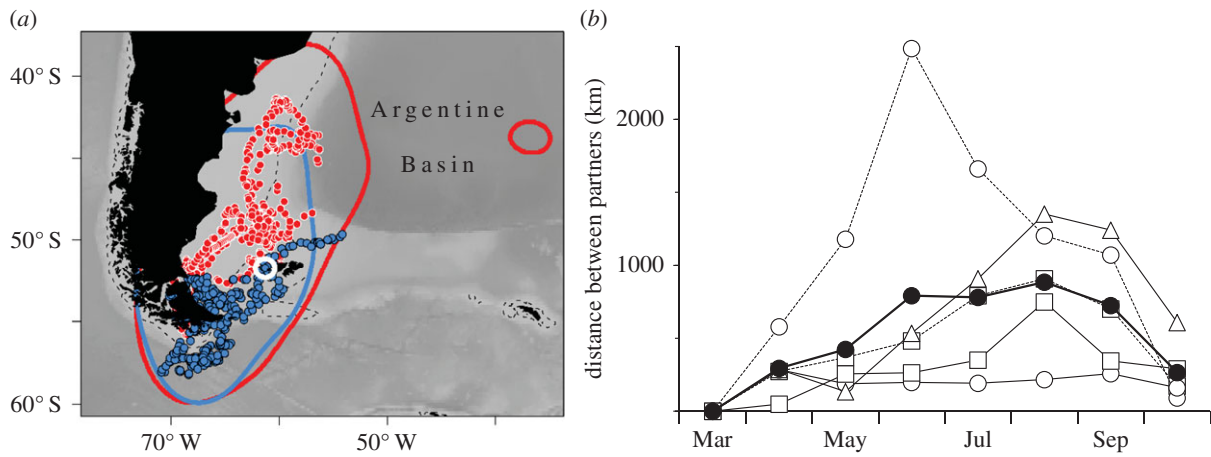


Figure 1. Winter migration of 13 southern rockhopper penguins surveyed from New Island (white circle) using GLS loggers. (a) Distribution area (95% kernel distribution contours) of males ($n = 6$) and females ($n = 7$) are shown with blue and red curves, respectively, and an example of one pair is detailed (blue dots circled in black: male; red dots circled in white: female). Background greyscale symbolizes bathymetry (darker for deeper areas), and black dotted lines show the 200 m isobath. (b) Monthly distance between location centroids of five penguin pairs (average of all pairs is shown in bold); values are mean \pm s.d. (Online version in colour.)

Table 1. Winter migration metrics ($n = 13$ birds, six males and seven females) for southern rockhopper penguins surveyed from New Island. Values are mean \pm s.d.

bird group	departure date	return date	time at sea (days)	maximum range (km)	total distance travelled (km)
all	4 April \pm 5 days	14 October \pm 5 days	194 \pm 7	999 \pm 476	17 219 \pm 6470
males	7 April \pm 3 days	11 October \pm 4 days	187 \pm 3	793 \pm 134	17 781 \pm 6291
females	1 April \pm 4 days	17 October \pm 3 days	200 \pm 4	1176 \pm 599	16 737 \pm 7081

approach with stable isotope analysis to provide explicit inferences regarding pair bonds throughout winter.

2. Material and methods

Study birds originated from a colony on New Island, Falkland Islands/Islands Malvinas (51.7° S; 61.3° W), where individuals of known sex have been surveyed since 2006 through systematic reading of individual, subcutaneous transponders [9]. We deployed leg-mounted global location sensing (GLS) loggers (weighing ≤ 6 g) on each mate of 10 penguin pairs when moulting was complete (24 March–6 April 2012). These loggers record light level, immersion and seawater temperature. Birds were recaptured and blood-sampled in October when they returned to breed. Their movements were estimated following a maximum-likelihood approach including latitude correction by seawater temperature, in the R package ‘tripEstimation’ [10] (see the electronic supplementary material, S1). Light-based geolocation provides two daily location estimates, with an expected spatial error of approximately 120–130 km for non-flying migrants tracked with the loggers we used [11]. Kernel utilization distribution contours were computed from location estimates, using ‘adehabitat’ in R with a search radius of 2° of latitude/longitude.

Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were measured on red blood cells (see electronic supplementary material, S2). Three additional pairs (six birds) were blood-sampled at the same time to increase our sample size. Isotopic half-life for $\delta^{15}\text{N}$ in red blood cells of rockhopper penguins was assumed to amount to 14.3 days, following experimental work on another penguin species of comparable body mass [12]. Because turnover rates are similar for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in endotherms [13], almost all blood C and N was renewed after

approximately 57 days (corresponding to four half-lives). Hence, the time integration of blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ corresponded to a two-month period before sampling, i.e. to the end of the winter tracking period. Isotopic niches were compared between sexes from Bayesian standard ellipses computed in the package ‘SIAR’ [14].

Paired and non-paired t -tests were used to investigate whether niche components differed between sexes and partners, respectively. Differences were considered as significant for $p < 0.05$.

3. Results

Sixteen birds (seven males and nine females, composing seven pairs from the previous season) were recaptured at their return on 7–21 October 2012. In all seven pairs, partners remained together for the new breeding season. Of the 16 retrieved loggers (80% of deployed GLSs), 13 were downloaded successfully (six from males and seven from females, composing five complete pairs).

The loggers indicated that females left the colony approximately 6 days earlier than males ($t_{12} = -3.08$, $p = 0.01$; paired data: $t_4 = 2.90$, $p = 0.04$), and returned approximately 6 days later ($t_{12} = 3.60$, $p = 0.004$; paired data: $t_4 = -6.74$, $p = 0.0025$; table 1).

Geolocation data showed wide-range (37.2–58.2° S; 32.8–72.3° W), dispersive migration of the penguins, mainly over the Patagonian Shelf (figure 1a). Although females seemed to distribute over a wider area than males, especially in the north, the distribution of both sexes overlapped markedly, and no statistical difference in maximum range reached or total distance travelled was found between sexes ($t_{12} = 1.64$,

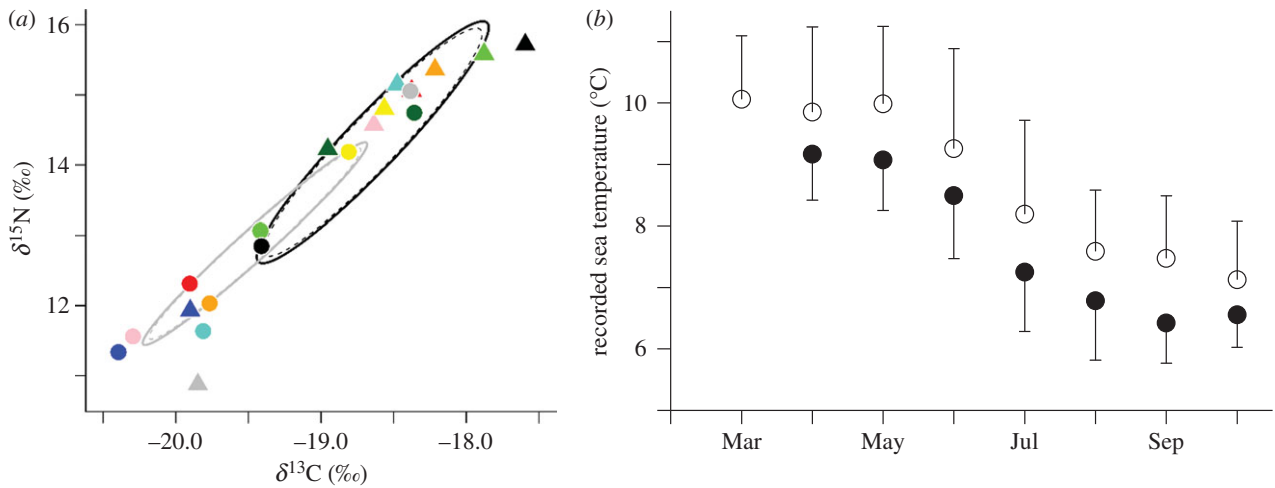


Figure 2. Southern rockhopper penguins' winter niche. (a) Blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of male (triangles) and female (circles) penguins from the seven GLS-fitted and three additional sampled pairs (pair mates share same colour). Standard Bayesian ellipse areas corrected (solid line) and uncorrected (dashed line) for small sample sizes are shown for males and females (black and grey lines, respectively). (b) Monthly seawater temperature recorded by loggers from males ($n = 6$; filled symbols) versus females ($n = 7$; open symbols); values are mean + s.d. for females and mean - s.d. for males. (Online version in colour.)

$p = 0.13$ and $t_{12} = -0.28$, $p = 0.78$, respectively) or partners ($t_4 = -1.94$, $p = 0.12$ and $t_4 = -1.10$, $p = 0.33$, respectively). Nevertheless, partners were systematically segregated over a large spatial scale: intermates distance averaged 595 ± 260 km across the non-breeding period and peaked at 885 km in August (range 216–1351 km among pairs; figure 1b). In one pair, this distance approached 2500 km in June, when the female moved to the Argentine Basin.

The birds' isotopic signatures showed a continuum of values, with a marked overlap between both sexes: the females' niche overlapped by 42% with that of males (figure 2a and see electronic supplementary material, S3). Within pairs, isotopic niches differed in $\delta^{13}\text{C}$ ($t_9 = 2.30$, $p = 0.047$) but not significantly in $\delta^{15}\text{N}$ ($t_9 = 1.90$, $p = 0.089$). Similarly, the recorded temperatures overlapped for both sexes during each month (all p -values > 0.05 ; figure 2b), but the paired females exploited significantly warmer waters than their partners, on average (April–October, $t_{34} = -2.38$, $p = 0.023$).

4. Discussion

Our results provide multiple evidence that throughout their winter migration, paired male and female penguins were spatially segregated over a larger scale than the expected error range of geolocation estimates. That partners were located hundreds of kilometres apart over most of the year did not prevent our study birds from re-pairing with their previous mates for breeding. Besides the seven pairs that re-united, two birds returned but mated with a new partner as the previous one did not return. Thanks to our individual long-term monitoring data [9], we are confident that the remaining four birds that were not detected did not return to the colony, but either dispersed to another colony or died at sea during winter.

Over their annual cycle, penguin mates seem to spend only limited time together. During the breeding period, colony-based observations ([6]; authors' personal observations from the 2006–2013 breeding seasons) indicate that partners reunite for approximately 20–30 days (day and night) from courtship to egg laying periods, approximately 2–3 days during the

incubation, and at night only during chick-rearing (over approx. 70 days). During the three weeks of moult spent ashore, partners may or may not re-unite at the nest ([6]; authors' personal observations). Partners then spend winter apart (this study). Overall, partners are together only during approximately 23% of the annual cycle. The high pair fidelity in these penguins thus cannot be explained by a prolonged time spent in close vicinity. However, these periods spent together occur at the nest exclusively, where the amount of elaborate pair-formation behaviour might affect mate retention [15]. In this respect, it is noteworthy that penguin species that do not build a nest have lower mate fidelity (in [4]).

In our study, the segregation of partners did not originate from a sex-based differential migration leading to exclusive winter niches (as opposed to other species [1,3]). Rather, our data showed that although females tended to distribute in warmer (i.e. more northerly) waters than males, the habitats exploited by each sex overlapped markedly, as depicted by the isotopic niches (figure 2a, see also [16]) at the end of the winter period. Stable isotope analysis showed that (i) there is a continuum of isotopic niches exploited by male and female penguins in winter, (ii) the isotopic niche of both sexes overlapped extensively at that time, (iii) for a given $\delta^{13}\text{C}$ value, both sexes had similar $\delta^{15}\text{N}$ values, suggesting that they fed on the same type of prey and (iv) paired males and females segregate in their isotopic niche, at least at the end of the winter period. That migratory animals may well demonstrate pair-wise segregation even in the absence of distinct, sex-specific winter niches brings the question of the proximate cause underlying this pattern. One mechanism may be the dispersive migration mode of the southern rockhopper penguin. This observation from our dataset is consistent with the large variation in individual routes shown by winter satellite tracking in this species [17]. Such dispersive migration, together with females leaving the colonies before the males, would hence result in partners being segregated de facto, without any exclusion mechanism. Given that parapatric populations over-winter in the same area [8,17], whereas sibling rockhopper species in the Indian Ocean conversely show directed migrations to population-specific wintering areas [7], this dispersive migratory behaviour may minimize potentially high levels

of local intraspecific competition. Hence, overlapping winter niches between sexes do not preclude segregation within pairs in monogamous migratory animals, and dispersive migration with sex-biased timings may yet be a sufficient proximal cause for generating this pattern.

Ethics. The study was performed according to Belgian and Flemish law and was approved by the ethical committee on animal experimentation (ECD, ID number: 2011/44).

Data accessibility. The penguin tracks are available on BirdLife International's seabird tracking database (<http://www.seabirdtracking.org/?q=Sphenisciformes>).

Authors' contributions. Study conception and design: M.P., L.D. and C.-A.B.; data acquisition, analysis and interpretation: all authors,

manuscript draft and revision: all authors. All authors approved the publication.

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Competing interests. We declare we have no competing interests.

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